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THE INFLUENCE OF SEX AND TREMATODE PARASITES ON CARRION RESPONSE OF THE ESTUARINE SNAIL *ILYANASSA OBSOLETA*

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ABSTRACT

The estuarine neogastropod, *Ilyanassa obsoleta*, was studied to determine the influence of sex and trematode parasites on the well-known tendency of this snail to aggregate on carrion. Fifteen experimental arenas (1 × 5 m) were delimited on the Cape Henlopen sandflat in Delaware Bay between July 1982 and November 1983. Snails (n = 2111) were examined by dissection. Frequencies of snails in specific categories of sex and parasitism in the arenas were determined before carrion was made available (expected frequencies), and these frequencies were compared with frequencies of the same categories among snails responding to carrion (observed frequencies). Experiments were categorized for analyses into breeding and nonbreeding temporal groups based upon the presence/absence of females with egg cases. Sexual condition alone affected carrion response. Uninfected females in reproductive condition tended to respond more frequently than predicted by controls (positive response) both during and after reproductive season, or else responded as predicted (neutral response). During breeding season males tended to show a neutral response and afterward to respond less frequently than expected (negative response). Parasite influence on carrion response was not detected until after the breeding season, at which time it was pronounced. Both sexes showed a positive response when infected with *Lepocreadium setiferoides*. *Zoogonus rubellus* and *Gynaecotyla adunca* infections produced negative responses in females but neutral responses in males. *Austrobilharzia variglandis* was inhibitory to females and probably to males as well. *Himasthla quissetensis* infections seemed not to affect response of either sex. Multiple infections were relatively frequent (9% of snails examined) and also influenced carrion response.

INTRODUCTION

Parasites in a variety of taxa significantly affect intermediate host behavior in a diversity of habitats (Rothschild, 1962) and these effects have been viewed primarily as parasite adaptations that increase the likelihood of transmission to the next host (*e.g.*, Carney, 1969; Holmes and Bethel, 1972; Moore, 1984). Behavior of animals with respect to nutritional resources in the environment is often studied (*e.g.*, Carr, 1967a, b; Crisp, 1978; McKillup and Butler, 1983) but there has been scant attention to the influence parasites might exert on such behavior, even when parasites are likely to be present [see Etges (1963) and Liebman (1983) for two exceptions]. Likewise, the importance of sex to resource utilization patterns is often ignored.

It is the purpose of this paper to report on a series of experiments carried out to determine the influence of sex and parasitism on carrion response in an important

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Atlantic (and Pacific) coast gastropod. Results indicate that sex and parasitism are indeed important influences on this host's behavior, and that future studies involving this (and probably other) species should take such influences into account. The Cape Henlopen sandflat on the western shore near the mouth of Delaware Bay harbors a large population of the mudsnail, *Ilyanassa obsoleta,* which sustains extensive populations of trematode germinal sacs (Curtis and Hurd, 1983). The attraction of *I. obsoleta* to carrion has been known at least since the work of Dimon (1905). Jenner (1956) surmised that since carrion was relatively scarce it could not be the main source of energy for such an abundant snail. However, it has been shown that carrion is more than an incidental nutritional resource since meat is required for survival, growth, and (at least) female reproduction in this snail (Curtis and Hurd, 1979; Hurd, 1985). Curtis and Hurd (1983) first noted that natural aggregations of *I. obsoleta* on carrion were sometimes predominantly female, and probably not a random draw from the available population. We speculated that differential response of the sexes to resources in the environment could explain some of the extensive spatial heterogeneity we observed in this seemingly homogeneous population. Present results support this by showing that males and females are differentially responsive to carrion. Also, since parasites can profoundly affect intermediate host behavior and there are several reports of the effects of trematodes on *I. obsoleta* ecology, behavior, and physiology (Sindermann, 1960; Vernberg and Vernberg, 1963, 1967, 1968; Stambaugh and McDermott 1969), we suggested that biologists might have to distinguish "apparent" (parasitized) and "functional" (unparasitized) snail individuals in experiments. Results to be presented unequivocally support this suggestion.

MATERIALS AND METHODS

Experimental sites

Carrion response experiments (CREs) were carried out in Lewes, Delaware, between July 1982 and November 1983. All but one were done on the Cape Henlopen sandflat. The features of this habitat and the *Ilyanassa obsoleta* population there have been described elsewhere (Curtis and Hurd, 1983). To see if carrion response was markedly different in a different habitat, one CRE was done in the nearby Canary Creek Marsh in one of the mosquito ditches where *Ilyanassa obsoleta* was abundant. This site was used in an earlier study (Curtis and Hurd, 1981) and is described there as the "high-marsh-ditch-site."

Experimental design

Approximately two hours (one on either side of low water) were available for each experiment. Before and after that period water tended to be too deep to work effectively. I chose sites on the basis of a steady ebbing current to carry stimulatory substances to the snails, a water depth of 10 cm or less for ease of observation, and an abundance of snails that would neither prove too numerous to dissect nor provide too few snails. Experiments were run throughout the period when snails were active (April–November).

The general plan of each CRE is as follows. Experimental arenas (1 × 5 m) were delimited from the surrounding sandflat with strips of hardware cloth (5 × 5 mm mesh). The hardware cloth fence was buried 3–4 cm in and stood 15 cm above the substratum, and served to exclude all non-arena snails. Arenas were set up with long axis in the direction of the water current. After setting up an arena I collected a control sample to measure frequencies of snails in various conditions of sex and parasitism in the arena population. Five 0.09 m^2 plots were sampled along each longitudinal half of the arena at 1 m intervals for a total of 10 plots. The sampling frame used in this procedure was subdivided with string into 5 × 5 cm squares which I systematically searched by eye and hand for *Ilyanassa obsoleta.* The first 10 snails encountered in each plot were retained separately for later examination. Other snails in a plot were counted but disturbed as little as possible. In cases where at least one but fewer than 10 snails were present in a plot, additional snails adjacent to the sampling frame were collected to make up the sample of 10 for examination. The 100 snails from the 10 plots within each arena served as a control sample for that particular experiment. Mean number of snails per 0.09 m^2 plot was extrapolated to provide an estimate of total snails in the arena. This estimate, minus snails taken as controls, provided an estimate of total snails available to respond.

Carrion used in CREs was either large commercial frozen shrimp or freshly opened hard clams, *Mercenaria mercenaria.* Carrion wet weight was recorded. After collecting the control sample, carrion was placed inside the arena just downstream from the upstream end. Carrion was fixed in place by pinning it to the substratum with a small wooden stake. A responding snail is one that under the experimental conditions moved to the carrion and began to feed. The moment of carrion placement was time zero and snails were collected as they arrived on the carrion for one hour afterward if current direction did not change and if snail activity permitted. Number of snails arriving in each 5-minute interval after time zero was noted. Responding snails were retained for later examination. Air and water temperature were measured. A refractometer was used to measure water salinity to the nearest g/kg.

In the laboratory, snails in responding and control groups were measured for shell height and dissected to determine sex, sexual condition, and presence or absence of parasitism. *Ilyanassa obsoleta* is dioecious and Smith (1980) provides a useful description of its reproductive system. Sexual conditions (following Hurd, 1985) were assigned to females according to presence of an egg capsule in a capsule gland (fec); presence of a capsule gland but absence of an egg capsule (fg); absence of a capsule gland and absence of any indication of a penis behind the right tentacle (f). Females in the fec or fg conditions are usually either reproductive (fec) or potentially so (fg). When out of the reproductive season, and/or when parasitized, females commonly appear in the f condition. Imposex females (Smith, 1980) were noted and recorded. Male sexual conditions were determined by assessing condition of the penis: mp males had a penis with size and shape characteristic of the species, while m males had a reduced penis (usually a bump or scar) and were nonreproductive.

Infection of snails in responding and control groups with trematode germinal sacs was also revealed by dissection. Stunkard (1983) reviewed the trematodes known to infect *Ilyanassa obsoleta* in the Woods Hole, Massachusetts region. His list encompasses (excepting the rare *Pleurogonius malaclemys*) the trematodes of *I. obsoleta* that I have observed in the Lewes, Delaware area; I have followed his nomenclature. As an aid to identification the plates of McDermott (1951) have been used. Species of trematode(s) (if any) infecting each collected snail was (were) recorded.

Analysis of data

Data available from each CRE include: experimental environmental conditions (temperature and salinity); wet weight of carrion used; an estimate of number of snails available to respond; size of each snail; frequencies of snails in various states of sex, sexual condition, and parasitism in a control group; frequencies of the same for snails in a responding group; and number of responders arriving on the carrion in each

5-minute interval of the experimental period. Since an estimate of number of snails available to respond was known, percent snail response could be calculated. Regression analyses were used to reveal significant correlations between percent response and water temperature, salinity, percent controls parasitized, number of snails available to respond, and wet weight of carrion presented.

A goodness-of-fit test was used to test the homogeneity of frequencies of snails in various states of sexuality and parasitism in responding and control groups. Experiments were combined into breeding and nonbreeding sets on the basis of fec presence/absence for this purpose. The test used calculates the statistic U (equivalent to χ^2) which is distributed approximately as Chi-square if expected frequencies are not too small (Powell, 1982). In calculating U ($= \Sigma \frac{(ob - e)^2}{e}$, where ob = observed and e = expected number of snails), I have used actual numbers of snails with various characteristics in the responding group as observed frequencies and used percentages in the control group to derive expected frequencies. If $P < 0.05$, the deviations between observed and expected frequencies were accepted as significant. Lastly, since dispersion of various categories of snails (*e.g.*, females, or snails infected with particular parasite species) could affect experimental results, frequencies of snails with certain characteristics in the 10 control plots were used to calculate within-arena coefficients of dispersion (Sokal and Rohlf, 1981) for a number of snail categories in experiments where none of the control plots was empty of snails (*i.e.*, 11/15 experiments).

RESULTS

Experimental parameters, snail size, and response pattern

Within-arena coefficients of dispersion for certain categories of snails were calculated for experiments where 10 control plots were collected and the category of snail in question was present. In the following list n = the number of experiments from which the mean coefficient of dispersion (CD) for the category of snail was calculated: females (n = 11, CD = 0.78); males (n = 11, CD = 0.7); not infected (n = 11, CD = 1.25); *Himasthla quissetensis*-infected (n = 8, CD = 0.92); *Lepocreadium setiferoides*-infected (n = 11, CD = 0.94); *Zoogonus rubellus*-infected (n = 11, CD = 0.77); *Austrobilharzia variglandis*-infected (n = 9, CD = 0.93). These CDs are all close to one and suggest randomness of distribution within experimental arenas for these major categories of snails. This indicates that composition of responding groups was not systematically affected by nonrandom distribution of snail types relative to carrion position.

Table I presents experimental conditions for each of the 15 CREs carried out in this study. Response was always below, and usually well below, 50%. Percent response is correlated in regression analyses only with water temperature ($r^2 = 0.29$, $P < 0.05$), with colder temperatures associated with reduced percent response.

The majority of snails involved in CREs were 20 mm shell height or more. Mean shell height (all CREs combined) was similar among responders and controls (21.8 mm, S.D. = 2.1 and 22 mm, S.D. = 1.9, respectively). Only 1.8% of all snails examined were 15 mm or less and their proportion was virtually identical among controls (1.7%, n = 1321) and responders (1.9%, n = 790).

Response to carrion was perhaps most frequent early in experiments but occurred more or less steadily throughout. Some CREs were terminated because of flooding currents (8/1/82, 8/7 and 11/5/83) and others (6/14 and 7/30/83) because no more snails were responding. In no CRE were numerous (>5) snails still approaching the carrion at termination, so one hour was sufficient to attract virtually all responsive snails in an experimental arena.

TABLE I

Environmental conditions [air (Ta) and water (Tw) temperatures, salinity (sal)], number of available snails, weight of carrion available, and percent of available snails responding during 15 carrion response experiments with Ilyanassa obsoleta

Date mo/da/yr	Ta °C	Tw °C	SAL g/kg	Carrion* type (g)	Estimated # snails available	Percent snails responding
7/4/82	20	30	22	shr (?)	(?)	(?)
8/1/82	28	27	30	shr (23)	2203	4
8/22/82	19	24	22	shr (15)	400	29
11/13/82	10	12	25	shr (19)	222	1
4/27/83	20	19	17	shr (14)	203	0
6/6/83	22	23	27	clam (24)	306	21
6/14/83	?	22	30	clam (32)	314	2
6/16/83	22	21	25	clam (78)	1311	4
7/20/83	26	35	22	clam (94)	272	30
7/26/83	31	31	28	clam (52)	229	15
7/30/83	22	24	26	clam (45)	140	9
8/7/83	34	33	23	clam (76)	4295	3
8/21/83	27	31	29	clam (51)	194	47
10/22/83	14	16	29	clam (45)	805	8
11/5/83	9	11	23	clam (30)	733	3

* Carrion was either commercial frozen shrimp (shr) or freshly killed *Mercenaria mercenaria* (clam). Wet mass (g) is given.

Sex and parasitism

Overall, 2111 snails were examined. For reference, total numbers in each category of sexual condition (with proportion parasitized) were: fec = 85 (4.7%); fg = 378 (25.4%); f = 724 (91.4%); mp = 295 (41.4%); and m = 630 (85.9%). Proportion of females with imposex features was 2.4%.

Results of individual experiments, broken down by sexual condition and parasitism, are presented in Table II. The marsh CRE (7/26/83) was not obviously unique and has been included with the sandflat CREs. Experiments were grouped for analyses into two categories. Presence of females with egg cases (fec) designates a breeding season CRE. Absence of fecs designates a nonbreeding season CRE. The 4/27/83 CRE was not included in either group for the following reasons. There was no response in this experiment (attempted twice at nearby sites with the same result), and field observations suggest that this had little to do with either sex or parasitism. Water temperature was high enough but salinity was low (Table I) because of recent rains. Snails tend to become inactive at salinities somewhere between 20–15 g/kg (Curtis and Hurd, 1980). Indeed, few if any of the snails in the general area were active at the time so the zero response was attributed to low salinity. In subsequent experiments salinities less than 20 g/kg were avoided.

One purpose of this investigation was to assess the effect of sexual condition on carrion response. As indicated above, some individuals in all sexual condition categories were parasitized. Effect of sexual conditions on carrion response was determined separately for uninfected and infected snails both in and out of breeding season (Table III). (Note: the terms positive, negative, and neutral will be used throughout as indicated below to describe carrion responses.) During the breeding season response of uninfected snails was affected by sexual condition. Females with egg cases responded to carrion more frequently than predicted by controls (positive response) while response fre-

TABLE II

Total numbers and frequencies (%) of Ilyanassa obsoleta *in 5 sexual and 10 parasitism conditions in control (CF = females, CM = males) and responder (RF = females, RM = males) groups from 15 carrion response experiments*

			Percent of total #														
			Sexual conditions					Parasitism									
Date mo/da/yr	Group	Total #	fec	fg	f	mp	m	Nl	Hq	Ls	Zr	Av	Ga	HZ	LZ	LG	O
7/4/82	CF	55	7	9	84			20	13	26	20	2		9	7		4
	CM	44				16	84	14	27	23	25			7	5		
	RF	27	22	4	74			33	11	22	17			11	6		
	RM	18				17	83	30	30	19	11			4	7		
8/1/82	CF	60	27	53	20			58	7	2	28	5					
	CM	40				50	50	63	5	8	18	2					4
	RF	50	27	35	38			54	8	11	27						
	RM	35				51	49	40	14	14	26	6					
8/22/82	CF	57		12	88			16	12	26	25	2		12	4		3
	CM	42				29	71	15	33	33	10	2		2		2	3
	RF	61		8	92			8	18	44	11	2		10	7		
	RM	55				11	89		25	42	16		4	7	5		
11/13/82	CF	60		12	88			20	25	20	17	3		12		2	2
	CM	40				50	50	20	28	20	18	5	2	5			2
	RF	2					100		50	50							
	RM	0															
4/27/83	CF	18		17	83			11	22	17	33		11			6	
	CM	22				32	68	18	14	14	32		9	4		4	4
	RF	0															
	RM	0															
6/6/83	CF	33	3	14	84			9	27	24	27			12			
	CM	66				22	77	8	18	17	27	4		11	9		6
	RF	36	3	3	94			3	17	20	33	6		14	6		
	RM	27				19	81	3	14	33	33			11	7		
6/14/83	CF	26	15	27	58			35		35	30						
	CF	14				43	57	36		36	28						

	RF	5	60		40			60		20	20						
	RM	1					100			100							
6/16/83	CF	48	31	48	21			77		2	15	2			2		2
	CM	52				73	27	69		6	17	2	4		2		
	RF	37	48	38	14			76	2	2	16				2		2
	RM	13				62	38	62			31						8
7/20/83	CF	55	5	4	91			11	20	25	36	2		4	2		
	CM	45				4	96	11	9	42	18			13	7		
	RF	46		2	98			15	22	41	13			4	6		
	RM	35				11	89	9	23	29	31			6	3		
7/26/83	CF	41		68	32			78		5	12			2			2
	CM	46				63	37	83		4	13						
	RF	21		52	48			81		5	14						
	RM	14				86	14	71			29						
7/30/83	CF	37		51	49			32		3	27	3	27			3	6
	CM	22				55	45	23			45		18			9	5
	RF	8		50	50			25	37	13	13		13				
	RM	4					100			25	50		25				
8/7/83	CF	50		92	8			74		4	22						
	CM	49				39	61	71	2	6	21						
	RF	91		88	12			77	1	1	21						
	RM	28				46	54	50	7	4	39						
8/21/83	CF	51		12	88			24	14	18	35	8			2		
	CM	49				14	86	16	18	24	34	2			4		2
	RF	47		15	85			36	15	19	17		2	4	2		4
	RM	44				18	82	23	23	18	23		2	5	5	2	
10/22/83	CF	51		8	92			4	12	20	14	8	6	22	2	10	2
	CM	48				6	94	4	23	12	15	4	12	15	6	4	5
	RF	40		10	90			7	25	27	17	3	3	10	3	6	
	RM	24				12	88	8	29	29	13		8	8	4		
11/5/83	CF	58		48	52			15	5	7	53	2	12	2			4
	CM	42				36	64	12	12	10	50	5	2		2		7
	RF	15		80	20			67	7	7	20						
	RM	6				33	67	17	17	17	33	17					

Fec = female with egg case, fg = female with capsule gland, f = female without capsule gland, mp = male with penis, m = male with penis stub, NI = not infected, Hq = *Himasthla quissetensis*, Ls = *Lepocreadium setiferoides*, Zr = *Zoogonus rubellus*, Av = *Austrobilharzia variglandis*, and Ga = *Gynaecotyla adunca*. Frequent double infections (HZ, LZ, LG) are indicated with the generic abbreviations of the species involved. Infrequent single and double infections are grouped under O.

TABLE III

Effect of sexual condition on carrion response of Ilyanassa obsoleta. *Shown are observed (ob) and expected (e) numbers of trematode-uninfected and -infected snails in carrion response experiments compiled into breeding season (A) and nonbreeding season (B) groups on the basis of presence/absence of females with egg cases (fec)*[a]

	Uninfected					Infected[b]			
A	fec	fg	f	mp	m	fg	f	mp	m
ob	42^{+}	23^{0}	8^{0}	26^{0}	7^{0}	10^{0}	118^{+}	13^{0}	84^{0}
e	22.6	29.6	6.4	37.6	9.8	17.1	95.2	13.9	98.8
	U = 22.9, d.f. = 4, $P < 0.001$					U = 10.7, d.f. = 3, $P < 0.025$			
B	fg	f	mp	m		fg	f	mp	m
ob	102^{+}	22^{0}	21^{-}	16^{-}		21	140	23	115
e	72.4	14.7	40.4	33.5		23.9	139.9	34.4	100.8
	U = 34.1, d.f. = 3, $P < 0.001$					U = 6.1, d.f. = 3, $P > 0.05$			

[a] Results of goodness-of-fit tests (U is equivalent to χ^2) are shown which test the null hypotheses that frequencies of snails in five sexual conditions among responders are not different than predicted by frequencies among controls. In significant tests cells with contributions to U of 3.84 or more [significant U ($P < 0.05$) with d.f. = 1] are marked (+) if snails in the category responded significantly more than predicted by controls, (−) if fewer than predicted responded, and (0) if they responded as predicted. See Table II for sexual condition symbols.

[b] Four infected control fecs were merged with the control fgs in the breeding season test.

quencies of other categories were not significantly different from those predicted (neutral response). Response to carrion by uninfected snails after the breeding season was also affected by sexual condition. Whereas females with capsule glands but no egg case (fg) were neutral during the breeding season, they were positive afterward. Uninfected males (mp and m) changed from neutral to negative since they responded significantly less frequently than predicted by controls after the breeding season. Uninfected females with no capsule gland (f) were neutral in both seasons. Among infected snails, sexual condition only affected carrion response during the breeding season, when f females demonstrated a positive response and other categories were neutral. The general result is that depending upon season, sexual condition, and infection presence/absence females tended to respond to carrion in a positive or neutral way while males, depending upon the same factors, tended to be either neutral or negative.

Table IV presents results of goodness-of-fit analyses which tested whether particular parasite species (and absence of infection) affected response of snail hosts to carrion. Three snail groups, consisting of (1) both sexes combined, (2) females only, and (3) males only, were tested for parasite influence both in and out of breeding season. Notably, during the breeding season responses of neither females nor males nor both sexes combined were influenced by parasitism. However, after the breeding season, parasites had a pronounced and unequal effect on carrion response of the two sexes. Uninfected females showed a positive response during this time while uninfected males demonstrated a negative response. Snails infected with *Himasthla quissetensis* were neutral. Both females and males infected with *Lepocreadium setiferoides* showed a positive response. *Zoogonus rubellus* and *Gynaecotyla adunca* infections resulted in a negative response among females but were associated with a neutral response among males. *Austrobilharzia variglandis* infections were inhibitory for both sexes combined and for females.

TABLE IV

Effect of trematode infections on carrion response of Ilyanassa obsoleta *in and out of breeding season*

	Parasitism categories										
	NI	Hq	Ls	Zr	Av	Ga	HZ	LZ	LG	O	U
I											
A	0.31	3.20	0.91	0.36	1.02	n.t.	1.21	0.01	n.t.	6.42	13.44ns
B	2.13^{0}	2.97^{0}	12.70^{+}	6.24^{-}	4.84^{-}	8.28^{-}	0.39^{0}	4.90^{+}	2.62^{0}	8.45^{-}	53.52s
II											
A	0.02	1.81	0.64	2.10	n.t.	n.t.	0.00	n.t.	n.t.	0.70	5.27ns
B	15.33^{+}	1.54^{0}	4.06^{+}	9.25^{-}	5.54^{-}	8.55^{-}	2.58^{0}	n.t.	n.t.	1.50^{0}	48.35s
III											
A	2.02	1.01	0.79	1.92	n.t.	n.t.	0.13	0.67	n.t.	1.96	8.50ns
B	6.50^{-}	2.58^{0}	10.34^{+}	0.02^{0}	n.t.	0.03^{0}	1.38^{0}	n.t.	n.t.	3.20^{0}	24.05s

Results for each cell in goodness-of-fit tests and overall U values are shown which test the null hypotheses that frequencies of categories of parasitism among responding snails are not different from frequencies predicted by controls in (A) and out (B) of breeding season. Results from tests on both sexes combined (I), females alone (II), and males alone (III) are shown. See Table III for explanation of +, −, and 0 symbols (n.t. = no test; ns = nonsignificant test, $P > 0.05$; s = significant test, $P < 0.001$) and Table II for parasite symbols.

Multiple infections (frequency among snails examined = 9%) also influenced carrion response, although not many of these categories were individually frequent enough for inclusion in tests (Table IV). *Lepocreadium setiferoides* (positive) and *Zoogonus rubellus* (negative in females) in the same snail produced a positive response (both sexes combined). However, when *Lepocreadium setiferoides* and *Gynaecotyla adunca* (negative in females) occurred together, positive and negative effects apparently cancelled producing a neutral response. The "Other" category includes a variety of infrequent single and multiple infections. Collectively, these produced a negative effect on carrion response (both sexes combined). Included in this category are snails infected with (singles) *Stephanostomum tenue, S. dentatum Diplostomum nassa,* and *Pleurogonius malaclemys;* (doubles) *Himasthla-Austrobilharzia, Himasthla-Gynaecotyla, Lepocreadium-Austrobilharzia, Zoogonus-Austrobilharzia, Zoogonus-Gynaecotyla, Zoogonus-Diplostomum, Austrobilharzia-Gynaecotyla,* and *Gynaecotyla-Diplostomum;* and (triples) *Zoogonus-Austrobilharzia-Diplostomum* and *Lepocreadium-Zoogonus-Austrobilharzia.*

DISCUSSION

Results show that response to carrion by *Ilyanassa obsoleta* is strongly influenced by a number of factors (not necessarily independent) including water temperature (Table I), season, sexual condition, and, not least, infection with trematode germinal sacs (Tables III, IV). Crisp (1978) has shown that recent snail feeding history is also important. Conclusions with respect to effects of sex and sexual condition on carrion response can best be derived from analyses of uninfected snails (Table III) since the confounding effects of parasites are eliminated. Males tend to be neutral during the breeding season and negative afterward. In contrast, females may be neutral (fg and f during, and f after the breeding season), but tend to show positive responses (fec during, and fg after). It is also of interest that sexual condition affected carrion response of infected snails only during the breeding season, when f females showed a positive response (Table III). Why should male and female response to carrion be so demonstrably different? Female reproductive activity (especially production of eggs and egg capsules) is energetically costly (Pechinik, 1979). In another neogastropod group (*Conus* sp.) Perron (1981) found that ova cost 6238 and capsule material 5442 cal/g. Since egg capsules are proteinaceous (Perron, 1981; Sullivan and Maugel, 1984) it follows that need for protein in the diet of females should increase. Hurd (1985) has shown that females require meat for reproductive output. The conclusion seems inescapable that females have an enhanced need for carrion during the breeding season and that this explains the positive response of fec females during that time (fg and f females discussed below).

Influence of trematode parasites is only evident after snail reproductive season and is not the same among males and females. Among females infection with *Himasthla quissetensis* produces a neutral response; infection with *Zoogonus rubellus, Austrobilharzia variglandis,* or *Gynaecotyla adunca* produces a negative response; and being uninfected or infected with *Lepocreadium setiferoides* produces a positive response. Uninfected males, on the other hand, are inhibited rather than stimulated as with uninfected fg females. Males infected with *Z. rubellus* or *G. adunca* are neutral rather than inhibited. Points of male-female agreement are that both infected with *L. setiferoides* demonstrate a positive response and both infected with *H. quissetensis* show a neutral response.

It is apparent that the effects of parasitic infection on this intermediate host are varied, species-specific, and not fully understood. Generally, intermediate host behavior changes of this sort have been interpreted as parasite-induced modifications to increase probability of transmission to the next host (*e.g.,* Holmes and Bethel, 1972; Moore, 1984). In the present case this reasoning seems not to apply because transmission from the snail is by cercariae, and usually to a second intermediate host which may then be ingested by a definitive host (various species of fish or birds in the case of *Ilyanassa obsoleta* trematodes). Other selective forces must be hypothesized to explain observed response modifications. Parasites obtain nutrition from hosts and it is to be expected that host nutritional state will be influenced. Wright (1966) has reviewed pathogenesis of helminths in Mollusca and specific studies of the effects of trematode germinal sacs on marine/estuarine prosobranchs have been made (*e.g.,* Rees, 1934, 1936; James, 1965; Cheng *et al.,* 1983; Sousa, 1983). In *Littorina littorea* germinal sacs block digestive gland tubules and create starvation effects. Even in unblocked regions of the gland glucose, glycogen, glycoproteins, and lipids were all reduced (James, 1965). If a snail is not seriously debilitated by its infection this suggests an explanation for enhanced response to carrion. In this study *Lepocreadium setiferoides*-infected snails, whose protein metabolism is altered compared to uninfected or otherwise infected *I. obsoleta* (Cheng *et al.,* 1983), demonstrated such a response and may serve as an example. The mechanism of such a behavior modification is obscure. The snail may respond as a consequence of simple starvation effects or the parasite may have a nutritional need of its own and secrete an allomone (Holmes and Bethel, 1972) to induce snail behavior. In either case, since parasitized snails are virtually always sterile (Curtis and Hurd, 1983), any adaptive value in the behavior must accrue to the parasite not the snail.

Negative responses on the part of infected snails are most likely explained by debilitating effects of parasites. Cheng and Snyder (1962) reviewed the extensive tissue damage associated with trematode infections in gastropods. Sinderman (1960) proposed that *Austrobilharzia variglandis* infections prevented *Ilyanassa obsoleta* from joining the migration to deeper water (Batcheldor, 1915) at season's end. My observation that snails infected with this species have a negative carrion response (Table IV) supports his contention. Moreover, Stambaugh and McDermott (1969) have shown that parasites (not including *Lepocreadium setiferoides*) make *I. obsoleta* move less often and more slowly than unparasitized controls.

A comparison of Tables III and IV makes interactions between sex and parasitism with regard to carrion response evident. For example, uninfected fg females have a neutral response during but positive response after the breeding season. My tentative explanation for breeding season neutrality is that perhaps the fg females involved had already made their egg cases and had reduced need for carrion (see fec discussion above). However, the postbreeding season positive response probably has more to do with being unparasitized (see NI IIB Table IV) than with being female. The only pronounced postseason fg response occurred in the 11/5/83 CRE (Table II) when water temperature was quite cold (Table I) and it may be presumed that healthy (unparasitized) snails were most able to respond (10/12 responding fgs were unparasitized). One of the most striking results in Table IV is the lack of parasite influence during the breeding season. Infected females in the f condition are an important illustrative point. In season, even though reproductively incompetent, these females nevertheless behaved the same as females in reproductive condition (fec) with respect to carrion (Table III). Out of season, f female carrion response was apparently influenced by other factors (Table III), and Table IV shows that parasites were prominent among these. Effects of parasitism are undoubtedly manifold (Wright, 1971), but whatever their effects it is remarkable that parasitized (sterile) females respond as reproductive individuals at one time of year and as parasitized individuals at another. This suggests some sort of dynamic balance (perhaps chemically mediated) between host and parasite influence on host behavior.

In this study multiple infections occurred in 9% of snails examined and involved a variety of doubles and two triples (Table II and Results). Ewers (1960), Vernberg *et al.* (1969), and Rohde (1981) studied marine/estuarine snails, and Cort *et al.* (1937) and Bourns (1963) studied freshwater snails in this regard. Vernberg *et al.* (1969) studied an *Ilyanassa obsoleta* population in North Carolina and found a multiple infection frequency of 0.02% among 5025 snails. These workers did not examine all snails by dissection and this (and perhaps small and/or large scale spatial heterogeneity as well) probably explains the magnitude of discrepancy between our observed frequencies. Two major points of agreement between this study and that of Vernberg *et al.* (1969) remain, however: *Himasthla quissetensis* and *Lepocreadium setiferoides,* though frequent single infections, never occurred together; and *Zoogonus rubellus* was involved in a large proportion of multiple infections. Dynamics of multiple infections have been considered by several authors (Cort *et al.,* 1937; Ewers, 1960; Bourns, 1963; Lie *et al.,* 1965; Vernberg *et al.,* 1969; Lim and Heyneman, 1972) and it seems certain that these patterns are biologically founded and merit further study.

Where multiple infections are abundant they can affect response to carrion. Indications from this study suggest that contributors to multiple infections can exert contrasting influences. The positive effects of *Lepocreadium setiferoides* apparently override the negative effects of *Zoogonus rubellus* but are neutralized by the negative effects of *Gynaecotyla adunca* (Table IV). This result suggests that outcomes of interactions between parasites (in terms of influencing host responses) in one snail are unique to the species involved, and makes interpretation of host behavior even more complex.

By now effects of parasites on intermediate host individuals or populations have been studied in a number of ecological contexts including terrestrial (*e.g.,* Carney, 1969; Moore, 1984), freshwater (*e.g.,* McClelland and Bourns, 1969; Holmes and Bethel, 1972), and marine/estuarine (*e.g.,* Swennen, 1969; Riel, 1975; Curtis and Hurd, 1983; present study) systems. More than 20 years ago Rothschild (1962) emphasized the impact of parasite-induced modifications of host behavior on almost any study of the host organism. While there is a growing knowledge of parasites and intermediate hosts there is nevertheless a tendency to underestimate the magnitude of influence parasites may exert. Results from the present study on carrion response are complex, and interpretable only because sex and parasitism were measured. A list of studies in which conclusions might have benefitted by incorporating an assessment of parasitism in experimental animals would be very long. Many authors conducting studies involving behavior of *Ilyanassa obsoleta* (or related snails) with respect to carrion and other environmental stimuli have basically ignored the possible influences of sex and parasites on experimental outcomes (*e.g.,* Dimon, 1905; Carr, 1967a, b; Crisp, 1969, 1978; Atema and Burd, 1975; Stenzler and Atema, 1977; McKillup and Butler, 1983). Curtis and Hurd (1983) showed that spatial heterogeneity with respect to sex and parasite frequencies can be very extensive, even in a seemingly homogeneous habitat. The present study shows that effects of sexual conditions and/or parasites on behavior can be substantial. Conclusions from past and future studies should be evaluated in this light.

Our knowledge of marine/estuarine parasites is probably the least among environments (Rohde, 1982). Results presented here and in other studies (cited above) indicate that ecological importance of parasites is to be more than merely suspected, and that biological knowledge will be well served by paying them more attention.

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